

THE BOTANICAL REVIEW

VOL. II

NOVEMBER, 1936

No. 11

CHROMOSOME STRUCTURE IN RELATION TO THE CHROMOSOME CYCLE

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Present conceptions of chromosome structure have resulted from a critical appraisal of diverse cytological interpretations in the light of genetic theory, for it has become increasingly evident that maintenance of the linear order of the genes through the mitoses depends on some permanent constituent of the chromosome. Such structure has been observed in several species of plants and animals as a slender coiled chromatic thread, the chromonema. Recognition that the chromonema carries the gene string, or genonema, has permitted correlation of the genetical and cytological findings.

Chromonemata were first discovered in 1880 by Baranetzky (2) as spiral bands in chromosomes of living sporocytes which he had pressed from anthers of plants of the genus *Tradescantia*. His contemporaries and immediate successors, however, derived other interpretations of chromosome structure, primarily from fixed material. In the early part of the present century chromonemata were described anew in such studies as those of Bonnevie (8, 9) and Vejdoický (114). Nearly all the investigators of that period regarded the chromonema as transitory in the mitotic cycle. About ten years ago Kaufmann (41) reported that the chromosomes of *Tradescantia* contain double spiral bands throughout somatic and meiotic divisions. Proof of the permanency of the chromonema has accumulated during the past decade, following the refinement of technical methods and the application of special procedures, and will be considered in the present article.

SOMATIC MITOSIS

The Structure of the Chromosome. For the study of somatic mitosis, plant cytologists have relied primarily on paraffin-imbedded

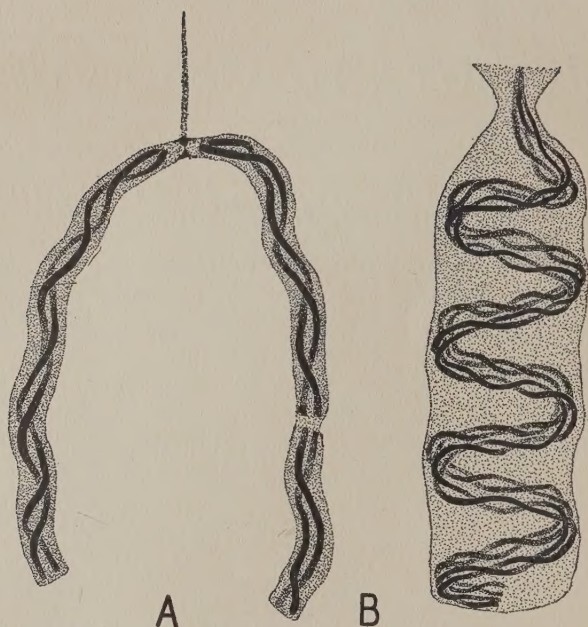


FIGURE 1A.—Diagram of somatic anaphase chromosome, with sub-median spindle-attachment region showing attachment chromomeres, and with secondary constriction in the longer arm. The chromonemata are represented as intertwined and embedded in a common achromatic matrix.

FIGURE 1B.—Diagram of one homologue of the *Tradescantia* type of bivalent at metaphase of the first meiotic division. Sister chromatids lie in close contact, and are coiled as major and minor spirals. Each chromatid is represented as consisting of a pair of intertwined chromonemata. All are embedded in the achromatic matrix.

and sectioned material. In such preparations the cylindrical metaphase and anaphase chromosomes often stain deeply and uniformly, except at the constrictions. These are relatively slender, achromatic regions, which are constant in position in a given chromosome (fig. 1A). Each chromosome has a spindle-attachment constriction, and may have one or more secondary constrictions. Within the attachment constriction, as is seen best in chromosomes with non-terminal spindle-attachment, are the minute granules, or "kinetic bodies", from which the "spindle fibers" appear to extend.

The arms of deeply stained chromosomes sometimes exhibit a moniliform contour which furnishes an intimation of the presence of chromonemata. Resolution of the spiral filaments is aided by such methods as prefixation (95, 77), freezing (21, 23, 24, 25) and differential staining. That the chromonemata exist in association with another substance, designated as the matrix, has been inferred not only from the direct observation of fixed and living chromosomes, but also from histochemical tests, which suggest that the spiral portion of the chromosome consists chiefly of nucleoproteins, the matrix mainly of lipoids (100, 97).

The chromonema, usually observed as a smooth thread of relatively uniform diameter, may appear at times as a linear aggregate of small chromatic particles, or chromomeres. They are seen most clearly when the chromonema is extended, as in the early prophase, and probably lie close together when the chromosome is contracted. Chromomeres are more pronounced in some organisms than in others, but when clearly defined they show a specificity of size and constancy of position which testify to their reality. Such true chromomeres, which present morphological evidence of the linear differentiation of the chromonema, are not to be confused with the chromomere-like aspect of delicately coiled threads (43, 27), nor with the dots and bands arising from the refraction pattern of a spiral (80).

The Number of Chromonemata. Despite the frequent observations of chromonemata, the number per chromosome at the different stages of mitosis remains a matter of controversy. The anaphase chromosome, for example, has been regarded by different investigators as composed of one, two or four chromonemata. Nor are these divergent opinions to be attributed solely to dissimilarity of the chromosomes of different genera,¹ since they have followed studies of chromosomes of the same genus. Substantial support has been given the interpretation that the anaphase chromosome contains two more or less intertwined chromonemata (42, 43, 95, 108-111, 26, 85, 29, 101, 48, 27), which persist through the telo-

¹ Nebel (82) suggests that the number of chromonemata may not be the same for all organisms. In the Diptera, the salivary gland chromosomes which undergo no further division have been interpreted as containing several chromonemata, which presumably arise from the original one without attendant chromosome division. Koltzoff (46) and Bridges (10) report that there are 16 chromonemata per "somatic bivalent" in *Drosophila melanogaster*; Bauer (3) reports 100-400 in certain Chironomidae.

phase and interphase to become the sister chromatids of the prophase chromosome. Each of these chromatids reveals a new split in late prophase or early metaphase to form the four chromonemata of the metaphase chromosome (42, 43, 108–111, 26, 85, 29, 101, 48, 27, 34, 35, 21).

The validity of certain other interpretations has been demonstrated less convincingly. According to Nebel (77, 79, 80, 82) and Stebbins (102) the quadripartite condition is recognizable in the telophase, and Nebel has suggested that each chromosome has four chromonemata throughout mitosis, although only two may be visible at anaphase. Recently, Goodspeed, Uber, and Avery (25), employing the Altmann freezing-drying technique have reported that the anaphase chromosome of *Lilium* contains four visible chromonemata, and the metaphase chromosome an 8-partite chromonematic complex.

At times only a single chromonema can be detected in anaphase and telophase chromosomes. This unitary condition often has been ascribed to lateral approximation of two or more chromonemata obliterating evidence of their individuality (42, 95, 29, 27). The explanation also has been offered that singleness at these stages represents the normal condition (13, 15, 16, 7) and that suggestions of multiple chromonemata follow either fixation artifact or cytological misinterpretation. Thus, Belling (7) contended that the appearance of duality in fixed material represents an artifact, since living resting nuclei contain unsplit threads, but this view is contested by the observations of Telezyński (109) and Kuwada and Nakamura (58) of twin chromonemata in living telophase chromosomes of staminate hairs of *Tradescantia*. Darlington's assumption that the aspect of duality rests on misinterpretation of optical sections of chromosomes disregards the contrary evidence of widely diverging chromosome ends, split satellites (106, 21) and end views to chromonemata. Objections of a decade or more ago to anaphasic duality (60, 50) attendant on the then current parasynapsis-telosynapsis controversy, were not concerned with the number of chromonemata, *per se*, but rather with the cleavage of the entire chromosome, which, it was held, would traverse the turns of the coils and disrupt the linear order of the genes (*cf.* 13, 16).

Treatment of chromosomes with x-rays has been employed in an effort to test the validity of these divergent interpretations of the descriptive cytologists. The experiments have proceeded on the assumption that if the chromonema is unsplit at the time of radiation, any alteration produced will be transmitted with the subsequent division of the chromosome equally to the daughter chromatids. On the other hand, unequal abnormalities would be expected from divided chromonemata, since each thread would be affected independently at the time of treatment. Mather and Stone (71) detected only chromosome breaks or equal abnormalities following irradiation of corms of *Crocus*, and concluded that the chromosomes are not split prior to the resting stage, when the rays apparently initiate the abnormalities (105). Failure to discover chromatid breaks is not sufficient proof, however, that the chromonema is undivided. Sax and Sax (93) note that the experiments conducted by Riley indicate that the split chromosome of *Tradescantia* behaves as a unit in response to x-ray treatment, since the microspore nuclei rayed during the resting stage show only chromosome breaks at metaphase. As Huskins and Hunter (33) have indicated, the further possibility exists that the broken ends of the chromatid may rejoin and thereby eliminate evidence of the alteration. Moreover, if radiation can affect either chromonema or matrix, as Mather (70) and Moore (76) have suggested, chromosome breaks may result from severing of the matrix and all the contained chromonemata, so that their subsequent behavior resembles that of an undivided thread.

By way of contrast, chromatid breaks furnish strong evidence that the chromosome is double at the time of irradiation. One such break was found by Lewitsky and Araratian (61) in x-rayed *Crepis capillaris*. White (116) detected both chromosome and chromatid breaks in spermatogonia of *Locusta migratoria* following irradiation of newly emerged males, although in his direct observation no trace of an anaphase split was encountered (contrast 75, 87). Huskins and Hunter (33), staining the chromosomes of *Trillium* to detect chromatid as well as chromosome breaks, found both types following irradiation of anthers containing cells in the second meiotic telophase or in the early resting stage. Since telophasic duality has been detected cytologically in root-tip chromosomes of *Trillium* (95, 34), the most convincing evidence from

radiation experiments indicates the existence of at least twin chromonemata during anaphases and telophases.

The Telophases: The Rôle of the Matrix. Chromonemata of stained preparations are differentiated more readily during the telophases than during the anaphases. Frequently this has been attributed to the loss of chromaticity or to the alteration of the matrix substance. Some observers have suggested that the matrix becomes continuous with the karyolymph of the newly formed nucleus, the chromonemata alone maintaining genetic continuity during the interphases (42, 95, 29, 27); others that the matrix remains associated with the coiled threads (4, 77, 79). Of the latter group Nebel holds the singular opinion that each spiral thread is sheathed in its own thick matrix, that under conditions of fixation the matrices may become confluent to simulate an investing material common to all the chromonemata. Then there is the theory that the matrix substance contributes to the formation of the nucleoli (see 96 for lit. cit., 64, 20, 74) which are developing synchronously with the skeletonization of the chromosomes. In this connection, McClintock (74) has reported that when the nucleolus-forming region of chromosome 6 of *Zea mays* is absent, or when its activity is impaired by certain chromosome deficiencies, the nucleus does not develop the large nucleoli typical of normal strains of *Zea*, but many small nucleolus-like bodies. These appear at indefinite positions along the chromosomes, apparently by the collection of droplets of the matrix substance. The evidence that the nucleoli form from the matrix is not conclusive, but "it is difficult to avoid the impression that a distinct relationship exists between the two" (74). Another activity attributed to the matrix is the formation of anastomoses (26, 74) which appear in many preparations as processes arising from the chromosomes and bridging the distances between them. Such outgrowths have been regarded more frequently as derivatives of the chromonemata (42, 43, 109, 111, 101, 29, 27, 25) or even as artifacts because of their variability or absence in certain preparations (79, 48).

Apart from explanations involving alterations of a matrix material in the anaphase-telophase transformations is the interpretation that loosening or extension of the coils suffices to render them more conspicuous. Darlington (15) has denied the existence of a matrix substance which occupies the spaces between the turns

of the coils, and Upcott (113) in support of this contention has presented an unconvincing analysis purporting to show that the entire volume of each chromatid is occupied by a tightly coiled chromatin thread.

When multiple chromonemata have been recognized in the anaphase or telophase chromosome they usually appear to be intertwined. It has been suggested, however, that the apparent intertwining may represent close approximation of independently coiled threads (25). In support of the latter alternative, Nebel (77, 79, 80) has made a comparative study of models of chromosomes composed of translucent materials, which he believes permits a more accurate appraisal of the microscopical images of chromonemata. His contention that the chromonemata of *Tradescantia reflexa* do not entangle at any stage is at variance, however, with the numerous observations of intertwined prophase and metaphase chromatids of *Tradescantia* as well as of other plant genera.

The Interphases; Continuity of the Chromonemata. As the irregularly shaped early telophase nucleus enlarges to assume a spherical form, the chromosomes become extended, their coils loosened. While retaining the telophasic arrangement at the proximal or spindle-fiber-attachment region, the arms of the chromosome lose their more or less straight arrangement, and are distorted into large loops or zigzags, which have been designated as super-spirals (16). Following this period of extension and attenuation the interphases are reached. The general appearance of the interphase nucleus, apart from the nucleoli, is of a network or reticulum, which is composed, according to most interpretations, of the chromonemata and interchromosomal processes. In some organisms, however, portions of certain chromosomes, often adjacent to the region of spindle-attachment, remain condensed and deeply chromatic (heteropyknotic) instead of contributing to the formation of the reticulum.

This period of transition from telophase to prophase presents the greatest obstacle to cytological verification of continuity of chromonemata. Darlington (13) has maintained that all direct evidence of structure in the resting nucleus is unreliable, but there seems little basis for doubt that the granules and rods so frequently observed in fixed material represent optical sections of chromonemata, as Martens (67, 68), Bělář (4) and Telezyński

(108, 109) found in living nuclei. In addition, less direct types of evidence of continuity are available (see 117, 4, 96 for lit. cit.). For example, the abnormalities produced following x-ray treatment of metabolic or resting nuclei furnish cogent evidence, as Sharp (96) has indicated, that even at these stages the linear organization of certain elements of the chromosome is normally maintained.

The Prophases. With the onset of the prophases, the reticulum-like aspect disappears; the chromosomes become more pronounced and are distinctly split longitudinally. To proponents of the theory of the undivided telophase chromosome, this represents the initial appearance of the split, and suggests that division occurs during the interphases (13, 16). Sister chromatids seem to be twisted about each other, but as the prophases advance and the chromosomes shorten and thicken, the amount of twisting decreases. An occasional wide separation of the chromatids during the middle prophases has been reported (95), although intertwining to some degree usually persists until metaphase (42, 109, 111, 101, 29, 85, 48, 27, 16). Meanwhile, along the chromatids, new coils become pronounced. Their doubleness and the consequent quadripartite nature of each chromosome may not be evident until late prophase or early metaphase, although actual division apparently occurs much earlier, the split being obscured by the close approximation in pairs of the half-chromatids.

Such questions as when and how the chromonema divides, how spiralling and uncoiling occur, will be considered later.

MEIOSIS

Structure of the Bivalent. Knowledge of the behavior of chromonemata during meiosis has accumulated primarily from the study of microsporocytes of plants with large chromosomes. The ease with which such cells may be expressed from the anther has permitted a wide array of observations both on living and treated material (see 96 for lit. cit.). Most frequently studied have been the compact bivalents of first metaphase. It will be recalled that such chromosomes of *Tradescantia* served as material for Baranetzky's original observation of the chromonema. Subsequently it was recognized that each of the spirals which he described represents a pair of closely appressed chromatids (42), the bivalent being a tetrad. In other genera, as in *Gasteria* (107), *Trillium*

(35) and *Fritillaria* (16), the tetrad structure is more readily discernible, since the paired chromatids are less intimately associated. The helical course of the chromatids defines the cylindrical form of the chromosome seen in the average sectioned and deeply stained preparation. End views, accordingly, appear as rings with the denser staining, or, if living, with the more refractive material peripherally disposed (11). In well-flattened smears a membrane or sheath may be identified, delimiting the chromosome and often removed some distance from the chromonemata (42, 35). Because of such evidence many observers have concluded that the axial region of the chromosome and the spaces between the turns of the coils is occupied by an achromatic matrix substance.

Such wide spirals as have just been considered may be designated as major spirals since recent observations have shown that they in turn consist of compact minor spirals. First recognized by Fujii (22), this spiral-along-the-spiral type of organization has been verified extensively; in *Tradescantia* (22, 37, 52, 54, 55, 57, 39, 92), in *Hosta* (37), in *Sagittaria* (99), in *Lilium* (99, 40), in *Trillium* (73), in *Fritillaria* (16). When the major spirals are unraveled artificially with ammonia vapor, presumably by removal of the matrix material, as Kuwada and Nakamura (55) demonstrated, the chromatids with their minor spirals present an aspect resembling a nucleus in interkinesis or interphase, except that there are no nucleoli.

Another recent advance in our knowledge of the structure of the metaphase bivalent has been the identification of eight chromonemata, resulting from the longitudinal splitting of each of the four chromatids (fig. 1 B). Observations of this "tertiary split" by Nebel (77), Huskins (30), Shinke (99), Iwata (reported by Kuwada, 53), and Huskins and Smith (35)² have been supported by certain radiation experiments. Thus, Marshak (65, 66) noted attached chromosomes at first anaphase in *Gasteria* which could be explained by the occurrence of a chromonematic division following irradiation at a four-strand stage. Moore's study of irradiation-produced mutations in the vinegar-fly, *Drosophila melanogaster* (76), indicates that each of the four chromatids at first meiotic metaphase in the egg contains two sets of genes in

² Also personal communications of Dr. Barbara McClintock and Dr. H. Dermen.

chromonemata or potential chromonemata, as do likewise the chromosomes of the mature sperm. Patterson (84) concluded, however, from a study of the effects of x-radiation on the production of mosaic flies by breaks in the X-chromosome, that this chromosome is split in about one out of every seven sperms. Moore has attempted to reconcile this conclusion with his findings by suggesting that chromosome breaks may represent a phenomenon of the matrix, so that "a break of an undivided matrix results in the severing of all the chromonemata, the behavior in subsequent inheritance suggesting a single chromatin thread."

The Leptotene Threads. To trace the origin of the eight chromonemata it is necessary to consider the prophases of the first meiotic division. Leptotene chromosomes frequently appear as single threads. This condition could result from failure of the chromosomes to split in the last pre-meiotic mitosis (30). There is, however, considerable evidence contrary to this view, since Smith (101), Koshy (47) and Hoare (27) report that the last pre-meiotic division of various plants does not differ from preceding mitoses with respect to the time of splitting of the chromonemata. In the Orthoptera, McClung (75) and Robertson (87) find the telophase chromosomes longitudinally split in the last spermatogonial division, which can be identified accurately. Moreover, a few observations of duality in leptotene threads have been recorded, those of Kaufmann (44) on *Tradescantia* and *Rhoeo*, of Koshy (49) on *Allium*, of Huskins and Hearne (32) on asynaptic oats and wheat, of Huskins and Smith (34) in portions of the chromosomes of *Fritillaria Meleagris*.³ The latter authors have found in *Trillium*, however, unsplit leptotene threads, and have attempted to reconcile these divergences by suggesting that the split occurs in those portions of the chromosomes which will not pair, the underlying theory being that synaptic attraction exists only between single threads (12, 30). Whatever the merits of such a theory when applied to forms in which pairing is incomplete, as in *Fritillaria*, asynaptic plants, and the interchange heterozygotes of *Tradescantia* and *Rhoeo*, it fails to explain the complete pairing of divided chromosomes, both meiotic (49) and somatic.

³ Lorbeer (Jahr. Wiss. Bot. 80: 567-818. 1934) reports that among the liverworts, the leptotene threads of *Sphaerocarpus Donnellii* are clearly double.

Best demonstrated in the Diptera, the phenomenon of somatic pairing has been studied carefully in *Drosophila melanogaster*. Anaphasic duality and prophase conjugation of split chromosomes with the resulting chiasma-like configurations have been detected cytologically (45), and there is genetic evidence of somatic crossing-over which occurs at a four-strand stage (103, 104).

Another explanation of the optically single leptotene chromosome involves the closing or "healing" of the pre-meiotic split. This seems a probable corollary of the attenuation and extension of the chromosomes at these stages. Inability to differentiate optically the intimately associated threads of fixed preparations is a matter of common cytological experience, and more recently Huskins and Smith (35) have recognized that doubleness or singleness may be a physiological and reversible state.

Leptotene threads of many organisms present the appearance of delicate beaded threads, because of the deeply staining chromomeres, specific in size and occupying corresponding positions in the homologues (see 86, 96, 94 for lit. cit.). In certain cases, chromomere-like aspects have been interpreted as effects produced by intertwining of sister chromonemata or by tight coiling (63, 44, 49). Koshy (49) reports that the two intertwined chromonemata become independent coils before synapsis.

Synapsis to Metaphase. Synaptic association often begins at the attachment constriction or at the ends of the chromosomes. Homologous chromomeres pair side by side to form the pachytene chromosome. According to Darlington (17), the parts of the chromosome which pair first condense first, as evidenced by the behavior of the proximal or spindle-fiber-attachment region of the chromosomes of *Fritillaria*. Pachytene chromosomes frequently are 7 to 11 or more times as long as at first metaphase (93, 66), and a certain amount of linear contraction may occur prior to coiling, as Belling (5, 6) noted in *Lilium*. During or at the end of pachytene, the equational split between sister chromatids becomes conspicuous, the chromosome presenting then a four-strand appearance. Diplotene begins with the separation of the paired chromatids, which reveals the chiasmata and whatever intertwining exists between the homologues. Huskins and Smith (35) and Darlington (18) have interpreted their preparations of these stages in *Trillium* and *Fritillaria*, respectively, as demonstrating that

separation on the two sides of a chiasma is always "reductional," that is, between homologues rather than sister chromatids, the chiasma resulting, therefore, from an exchange between two chromatids of partner chromosomes (the one-plane theory). Such accurate identification is extremely difficult in most plant material, although extensive studies of this kind have been made on the Orthoptera, where, according to McClung and his students, opening out of the chromatids occurs along the equational as well as the synaptic plane (the two-plane theory).

As diplotene progresses, the chromosomes shorten, thicken, and assume a moniliform contour. Evidently spirals are developing, but their relation to the major and minor spirals of metaphase is less certain. Darlington (18) interprets mid-diplotene spirals of *Fritillaria* as minor ones. They are presumably complete by late diplotene, whereas the major spirals are first discernible at that stage, and are not complete until diakinesis. According to the interpretation of Kuwada and Nakamura (54, 53), the major spirals of *Tradescantia* are established first, the minor spirals resulting from the secondary coiling of the strand which forms the spiral. Sax and Sax (93) state that the minor spirals appear to begin development before the major ones, but that they may develop so slowly that they continue to coil, or at least contract, after the major spirals are established in early metaphase. In *Trillium erectum*, Huskins and Smith (35) find that the major spiral is established in mid-late diakinesis. No evidence of a compact minor spiral was observed, although the coiled chromatid twists on its axis and is loosely waved somewhat like the minor spiral of Nebel (77). In *T. kamtschaticum*, however, both the major and minor spirals have been observed by Matsuura (73).

At diakinesis the strongly contracted chromatids are spiralled in pairs except where they change partners at the chiasmata. Resolution of the chiasmata may not occur until anaphase, as in *Trillium* (35), although in many species the dyads are connected at metaphase only by their ends. The significance of the matrix in maintaining such pairing has been emphasized by Sax and Humphrey (92), Huskins and Smith (35) and Sax (91). The number of major spirals seems constant in a given homologue at metaphase (90, 107, 78, 39). Matsuura (73) reports that in *Trillium kamtschaticum* the pitch of the coils is the same in all of the five

bivalents, and concludes that the length of the chromosome is a function of the number of spiral gyres. During late metaphase the closely appressed chromatids of the *Tradescantia* type of dyad become more widely separated, without entangling or extension of the major coils. In *Secale*, however, the major spirals tend to straighten out before the paired chromatids separate in late metaphase (90). Since this occurs without elongation of the meiotic chromosome, the drawing-out of the major coils has been attributed to the development of the minor spirals at this stage (93).

Anaphase I.—In early anaphase as the proximal regions of the dyads move apart, the distal remaining in contact, the major coils may be pulled out temporarily, but with the release of tension the spirals again contract. The direction of coiling, especially clear at these stages, is evidently not a stable or genetic character (91, 81, 82). Sister chromatids of *Lilium* with terminal spindle-attachment may both coil in the same direction, either dextrorsely or sinistrorsely; they may coil in opposite directions; or, the direction of coiling may change along one or both of the chromatids. Iwata (38), in making this analysis, found that the four classes occur with about equal frequency. In chromosomes with non-terminal spindle-attachment, coiling is frequently in the same direction in both arms (90, 78, 92). When the direction of coiling reverses, it is usually at the spindle-attachment region, occasionally along the arms (90, 107, 38, 35, 91). Such changes between spindle-fiber and distal end occur in *Trillium* almost invariably in equivalent positions in two of the four chromatids, and are about twice as numerous as the chiasmata at diakinesis or metaphase. Therefore, Huskins and Smith (35) have noted that such changes of direction, associated with chiasmata, are related, though probably only facultatively, to crossing-over. To test the relationship between coiling and the mode of crossing-over, Nebel and Ruttle (83) have studied the direction of coiling at first metaphase and anaphase in sporocytes of *Tradescantia reflexa*. They interpret their observations as favoring the two-plane theory.

The Second Meiotic Division. At late anaphase the paired chromatids, closely associated only at the spindle-fiber region, form characteristic V- or cross-shaped figures. Following their movements to the poles the strongly contracted chromosomes may pass directly to metaphase of the second division, without material

change in structure, as in *Trillium* or in the abnormal *Gasteria* studied by Tuan (112), but more commonly nucleus formation intervenes. Loosening of the major coils attends the extension and adjustments of the chromosomes in the enlarging nucleus, but the degree of interkinetic uncoiling may vary in different plants, or even in different chromosomes. At second metaphase the chromosomes may show only minor coils, as in *Tradescantia* and *Rhoeo* (92, 39, 91, 93), or both major and minor coils, as in *Sagittaria* (99) and *Fritillaria* (16). In certain species of *Lilium* (40) and *Vicia* (93) some chromosomes may show major and minor spirals, others only minor ones.

The anaphase or telophase chromosomes of the second meiotic division have been described as two-parted in *Allium* (48), *Gasteria* (107), *Galtonia* (101), *Rhoeo* (91), *Scilla* (27), *Tradescantia* (58) and *Trillium* (35). Kuwada and Nakamura (58) find that these paired chromonemata of *Tradescantia* are not twisted about each other; they have been described as intertwined in *Allium* (48), *Galtonia* (101) and *Scilla* (27). The anaphase-telophase split of the second division between chromonemata which are to separate at anaphase of the first postmeiotic division is probably referable to the "tertiary split" of the first meiotic division, but is sometimes not evident prior to the prophases of the second division (107, 101, 48, 27).

First Postmeiotic Division. There have been but few studies of chromosome structure during the first division in the microspore. In *Fritillaria*, according to Darlington, the prophase resembles a somatic prophase except that the superspirals are more clearly developed. In *Trillium*, Huskins and Smith find that the metaphase chromosomes are quadripartite, the anaphase chromosomes double. In *Tradescantia*, Sax and Sax find some evidence that the metaphase and anaphase chromatids contain two threads which are coiled together.

CHROMOSOME MECHANICS

Spiralization. Chromonemata usually are observed as coiled threads. Apparently somatic chromosomes are not devoid of coils at any phase of mitosis. In meiosis, apart from the chromomeric aspect of leptotene and early postsynaptic stages, coiled chromonemata are conspicuous throughout the first and second divisions.

In the sequence of mitoses it seems, therefore, that the old coiling is reduced and disappears as the new coiling comes to completion. Accordingly, it has been suggested that the new spirals aid in drawing out the coils persisting from the previous division (56, 58, 93). This process is related to the fact that in general the maximum number of turns of a spiral obtainable in a thread depends on its length and thickness. When the thread is shortened and thickened, the number of coils is reduced. In a double-stranded spiral the number of twists between the strands is equal to the number of turns of the spiral, and will be reduced as the strands shorten and thicken. Thus in the somatic prophase new coiling causes shortening and thickening of the chromonemata, with the gradual reduction of the old coiling and of the twisting residual from the preceding telophase (58). Kuwada (53) suggests that twisting of the chromonema leads to coiling and seems to be determined primarily by an internal factor, with the contraction of the matrix playing an accessory rôle. Comparison is made between chromonema coils and those of the tendril which are due to internal twisting, and which show the types of coiling with respect to direction observed in chromosomes. The interlaced condition of anaphase and telophase chromonemata is regarded as supporting evidence for the hypothesis of coiling by internal twisting, the assumption being made that the half chromatids coil together during the prophase. Concerning the probable method of formation of the double-coiled, double spiral of the first meiotic division, the explanation is offered that early prophase coiling draws out the old or residual spirals, that each chromatid coils independently so that the two major spirals do not interlace, and that as the minor spirals are established, the major ones are not drawn out because of the contracting force of the matrix (54). To this secondary coiling is attributed, however, the untwisting of the two intertwined chromonemata of each of the four chromatids of first prophase in such plants as *Tradescantia reflexa*, in which the chromosomes of second metaphase and anaphase show parallel but independent spirals (58). The occurrence of intertwining chromonemata in other plants at second anaphase is ascribed to division or separation of the half-chromatids at a later period in the first division than occurs in *Tradescantia*, possibly after the secondary coiling has been completed (58).

Splitting of the Chromonema. A problem related to coiling is that of the time and method of splitting of the chromonema. As indicated in the first section of this paper, there are various interpretations concerning the period at which the split first becomes visible. In some plants this seems to be at about the time that spiralling begins (35, 93). Sax and Sax (93) are of the opinion that the split occurring in each of the chromatids during mitotic prophase causes them to coil independently, whereby the remnant coils of the preceding anaphase are removed. Huskins and Smith (35) find that in both mitosis and meiosis the spiralling begins more or less coincidentally with the first appearance of the split in the chromatids, and have presented their "heterogonic growth" theory of spiralization. They have accepted Kuwada's earlier explanation of the pattern of coiling, namely, that for each turn of the spiral there is a twist of the two threads about each other in the opposite direction, so that the two coiled threads may separate, without entangling or uncoiling, as occurs in the dyad of *Tradescantia* at late first metaphase or at anaphase (51). They have observed that the half-chromatids of *Trillium* are twisted about each other shortly after the appearance of the "tertiary split" of the first meiotic division. If growth in thickness of the half-chromatids then occurs during the metaphase and anaphase on the outer side of the chromatid, it will occur spirally around them with a reversal of direction once in each gyre of the chromatid spiral, and will be on opposite sides of each half-chromatid in each successive gyre. The heterogonic growth, together with the tension produced by syneresis, will provide a self-perpetuating mechanism for spiralization. Sax (91) has pointed out, however, that the transition from about five major spirals of the first meiotic division to the 20-25 minor spirals of the second division in *Tradescantia*, and comparable behavior in *Rhoeo*, is difficult to reconcile with this hypothesis.

Kuwada and Nakamura refer the split in each chromatid to the interphase, and note that if the halves are still intimately associated when coiling begins in the prophase, they will twist about each other, but should they separate and coil independently no aspect of interlacing will be presented. Darlington (15) likewise holds that splitting occurs at interphase, although one mitosis later than that postulated by Kuwada and Nakamura. On the contrary, the

8-partite metaphase chromosomes of *Lilium* observed by Goodspeed, Uber, and Avery suggest that division may occur approximately three mitotic cycles before separation is accomplished. These investigators conceive of gene division as occurring at the end of the resting stage, with the succeeding prophase and early metaphase devoted to an elaboration of a visible chromonema.

Since in somatic mitosis the chromosomes do not appear free of coils at any period, full extension of the chromonema apparently is not prerequisite to its longitudinal division. A plane of division in a coiled thread, which follows the turns of the spiral, will lead to intertwined halves (*cf.* 48, 27). Darlington (18) suggests that division involves the splitting of one large thread into two equal small ones in such a way that the two if straightened without rotation of the ends would lie in one Euclidean plane. Then there is Nebel's contention that the chromonemata do not entangle at any period. To account for this condition he has suggested that regardless of the time of reduplication, if it occurs in only one plane, passing through the main axis of the chromosome, no difficulty will arise in separating the daughter chromonemata even if they are coiled spirally (81).

Coiling and Crossing Over; An Hypothesis. The analysis of the internal mechanics of chromosomes presented recently by Darlington (16-19) involves his interpretation of the various types of coils observed during mitosis and meiosis in *Fritillaria*. The property of the formation of spirals is attributed to an internal twist due to a rearrangement of the constituent particles, either between molecules, or within molecules. This molecular spiral is a compensating twist and leads the thread to coil in an internal spiral in the opposite direction to that of the major and minor spirals. The direction of the molecular spiral is subject to unitary control in each of the arms of the chromosome. In somatic mitoses the anaphase and telophase spirals do not relax completely prior to the resting stage when division into paired chromatids occurs. The spirals are uncoiled gradually during the prophases, and as a result the two chromatids become twisted about each other in the opposite direction (the so-called relational spiral). In meiosis the prophase begins precociously, before the chromosomes have divided and before they have reached their maximum extension. Consequently, the two homologues coil round one another to compensate for any

uncoiling which has survived the leptotene stage. As the molecular spiral continues to uncoil during pachytene beyond what is necessary to straighten the chromosomes, there is produced a system in which, when the chromosomes divide, they will be twisted around one another in the opposite direction to that in which they are coiled internally. The four chromatids are therefore in a state of tension resulting from the conflict of lateral attraction and longitudinal cohesion. This state of tension may be relieved by breakage of one of the two chromatids of each homologue at corresponding levels. Genetically this leads to crossing-over; the union of the broken ends to a recombination. Crossing-over is regarded, therefore, as replacing relational coiling.

At variance with the postulates on which this hypothesis rests are the numerous observations of multiple chromonemata at all stages of mitosis and meiosis, the occasional observation that changes in direction other than those resulting from crossing-over occur in chromosome arms, the finding that the major and minor spirals may coil in opposite directions (38, 92a). It is evident, therefore, that the various and often antithetic conclusions concerning chromosome mechanics are conditioned by the diverse cytological observations on which they rest. Accordingly they must be regarded as provisional until a greater number of data, observational and experimental, are offered to test their validity. In the meantime they serve as important steps in the growing efforts to interpret chromosome structure in terms of behavior.

CONCLUSIONS

The observational and experimental evidence reviewed here indicates that the chromonema is a fundamental and permanent component of the chromosome. As a structure persistent through the mitotic cycle, it provides a mechanism for the maintenance of the linear order of the genes, its chromomeric organization furnishing morphological evidence of its linear differentiation. Other theories of chromosome structure, which regard the chromonema as transitory in the mitotic cycle, are inadequate in light of present knowledge of chromosome behavior and genetical function.

With respect to the number of chromonemata per chromosome, the bulk of evidence favors the interpretation that the somatic metaphase chromosome is 4-partite, and that the bivalent of the first

meiotic metaphase is 8-partite. The chromonemata of such somatic chromosomes are coiled in minor spirals, those of the meiotic bivalent in both major and minor spirals. Relatively little is known of the behavior and rôle of the achromatic matrix material with which the contracted chromonemata usually are associated.

Studies of chromosome structure during meiosis have been made primarily on the metaphase bivalents, when the chromonemata are defined most clearly. An accurate knowledge of the organization of prophase chromosomes is essential, however, to critical analysis of such phenomena as synapsis, chiasma formation and crossing-over. In several of the recent studies, efforts have been made to trace the chromonemata through the first meiotic division, but evidence on the structure of leptotene and pre-leptotene chromosomes remains meagre. Additional cytological investigations of these stages will furnish a more substantial basis than now exists for such speculations concerning chromosome mechanics as are indicated in the preceding section of this paper.

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GLOSSARY ADAPTED IN PART FROM DARLINGTON'S

"RECENT ADVANCES IN CYTOLOGY"

- anaphase:** the stage of a nuclear division subsequent to metaphase and previous to telophase, during which daughter-chromosomes move apart.
- bivalent:** a group of two homologous chromosomes.
- chiasma (ta):** an exchange of partners amongst four chromatids associated in pairs.
- chromatid:** a half of a longitudinally split chromosome.
- diakinesis:** the last stage in the prophase of the first meiotic division, immediately before the disappearance of the nuclear membrane.
- diplotene:** the stage following pachytene in the prophase of the first meiotic division, during which the chromatids of the tetrad widen out in pairs, so that the four chromatids become plainly visible.
- dyad:** the univalent chromosome, composed of two chromatids, at meiosis.
- heterozygote:** an organism derived from the union of gametes dissimilar in respect of their chromosomes.
- homologue:** one of two homologous chromosomes, i.e., those contributed by the two parents and influencing the same characters.
- interkinesis:** the resting stage which may occur between the first and second meiotic divisions.
- interphase:** the period between two rapidly succeeding mitoses.
- karyolymph:** the nuclear sap, or ground-substance of the nucleus.
- leptotene:** the long slender chromosome threads of the early prophase of the first meiotic division, just before synaptic association; also the stage itself.
- meiosis:** a form of mitosis involving two nuclear divisions, during which the chromosome-number is reduced from diploid ($2n$) to haploid (n).
- metaphase:** the stage of mitosis or meiosis in which the chromosomes lie in a plane at right angles to the axis of the spindle and half-way between the poles.
- nucleolus:** a body in the nucleus which disappears during nuclear division.
- moniliform:** jointed or constricted at intervals.
- pachytene:** the thick bivalent thread (and the stage at which it occurs) produced by pairing of chromosomes in the prophase of the first meiotic division. This stage is followed by diplotene.
- parasynapsis:** side-by-side association of chromosomes during nuclear division.
- spindle-attachment:** the point in a chromatid which moves first to the pole at anaphase.
- satellite:** a segment of a chromosome, separated from the rest by one long constriction if terminal or two if intercalary.
- telophase:** the last stage of nuclear division, after movement of the chromosomes has ceased.
- telosynapsis:** the alleged end-to-end union of the chromosomes (synaptic mates) in synapsis. The end-to-end arrangement of chromosomes observed in some organisms at late prophase or at metaphase is now regarded as derived from earlier parasynaptic association. See discussion in Cleland's article, *Bot. Rev.* 2, p. 341.

PHAEOPHYCEAN LIFE-HISTORIES IN RELATION TO CLASSIFICATION¹

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It is safe to say that our knowledge of no other great plant group has broadened more rapidly and with more startling changes in the present century than has that of the algae. As these plants are of great economic importance, for the most part either indirectly or in the mass, it is not surprising that the bulk of modern researches on algae has either been ecological or plankton studies or has been directed toward problems bearing on classification. Classification is, of course, a common approach to the study of a plant group. In spite of a quite extensive recognition of species differences, marine algae were classified into *Conferva*, *Ulva* and *Fucus* till long after Linnaeus' time and in works as consequential as Sowerby's "English Botany" (First Edit.) and Dawson Turner's "Historia Fucorum" early in the 19th century. Immediately thereafter these groups of species were broken down into genera of the modern type; much later, reassembly of these into tolerably rational families and orders was accomplished by the efforts of several investigators so that orderly compendia became possible, like J. Agardh's "Species, genera et ordines algarum." The classification of Phaeophyceae was the slowest to respond to studies relative to life-history and cytological state. However, about twenty years ago the publications of Sauvageau (19, 20, 21) and but little later of Kylin (10) began to throw such surprising light on life-histories of the kelps that the fundamental classification in this group had to be overhauled. Research in the Phaeophyceae during the last twenty years has concentrated largely on experimental studies. Some purely chemical, some physiological, most of them have been developmental and their result has been so to broaden and redirect our knowledge of the morphology of these plants as to fundamentally alter our major systematic concepts in the group. There has been relatively little strictly taxonomic activity, little of mono-

¹ Papers from the Herbarium and the Department of Botany, University of Michigan, No. 589.

graphic revision, and that which is cytological in trend has largely been crude and applied to the problems of development. Genetical interest has not yet been awakened in the group.

The importance of life-history studies in outlining major features of classification of the Phaeophyceae developed much more rapidly after the discovery of the gametophytes in the kelps. An alternation of similar gametophyte and sporophyte phases had been recognized for *Dictyota* (5) and of dissimilar phases in *Cutleria*, but this did not stimulate any fundamental revision. When Sauvageau, and then Kylin and others, discovered that *Laminaria* and its relatives (kelps) had microscopic oogamous gametophytes, it became clear that an experimental study was needed of every plant lacking, in the morphological sense, either sporangia or gametangia, or at least in each family and genus of a number of species sufficient to fix the character of that group. Latent enthusiasm for experimental studies on marine algae broke out in a large number of papers, first on the kelps and then on other Phaeophycean groups. For various reasons most of these were incomplete studies, since contaminations (chiefly diatomaceous) and maintenance of a suitable rather low temperature rendered it hard to maintain cultures long enough (several months) to get the full history. Cytological confirmation of the significance of the developmental sequences in particular is usually lacking. In fact, the cytological data respecting Phaeophycean life-histories are, from the standpoint of the cytologist, badly worked out, showing every evidence of lack of technical mastery. The material appears to be somewhat difficult to handle, so that at best all that can now be demonstrated is the chromosome count in the subject.

The general result of these cultural studies has been to show that many Phaeophyceae possess phases which are relatively minute in stature. Some of these are cytologically obligatory alternates in the developmental cycle; more generally they are not. In the latter case they may represent ecologically advantageous conditions somewhat comparable to the protonema of a moss. Some have no reproductive functions and only grow to the adult plant directly and vegetatively, although when branching they multiply the points of origin of the more massive growth stage. Others have reproductive functions, and it is not surprising that such individuals should be

repetitional, with the possibility that several generations might succeed each other before the incidence of the massive stage.

Lacking comprehensive evidence to the contrary, it appears that these repetitional phases do not involve any change in chromosomal number. Passing into the massive stage without any such change, they are not to be considered as essential factors in the gametophyte-sporophyte cycle, since the massive stage is either continuous in growth with the minute stage or else bears the same type of reproductive organ.

It is frequently reported that the minute stage is functionally different in its reproduction from the succeeding massive stage growing from it. For instance, where both have plurilocular organs, those on the minute stage function as fertile gametangia while those on the massive stage produce neutral zoöspores. This may well be true as to their functioning under experimental conditions, but that it is always equally true under natural conditions is a dangerous assumption. There is so little known as to the best conditions for maintaining these cultures, particularly for sexual fusions, so little uniformity and reproduceability of results, so much relation perhaps with the season at which they were set up, that inferences should be drawn from them only with the greatest caution. Particularly is it unwise to attribute obligate limitation of sexual functions to such stages when the massive phase bears morphologically similar reproductive organs. The evidence that under other conditions these massive stages may not be sexually fertile is negative in nature and so, on such a question, inconclusive.

It is perhaps well to consider here to what degree the conceptions of sporophyte (a $2n$ or diploid plant) and gametophyte (an n or haploid plant) can be applied to the Phaeophyceae. We have no conditions comparable to those in the higher Rhodophyceae where the haploid sexual plant supports an epi- or endophytic diploid multiplicative carposporophyte which is largely parasitic and largely, if not wholly, lacks vegetative tissues. The ameiotic spores of this sporophyte give rise to a second, now independent and diploid tetrasporophyte, similar in vegetative aspect to the gametophyte and climaxing in the meiotic production of spores in tetrads (quartets). Even with this distinctive morphological alternation of three generations the greatest care must be exercised in assumptions involving the haploidy or diploidy of

any tissue. We have genera (like *Callithamnion* and *Spermothamnion*) where sexual organs and tetraspores appear on the same plants; others where the carposporophyte (some *Liagora* and *Phyllophora* species) is closed by the production of tetraspores (presumably meiotic); and finally others (in Bangioideae and the lower Florideae) where meiosis precedes carposporophyte development so that it is haploid from the start and the tetrasporophyte is absent. It is plain from the conditions in the Rhodophyceae that the morphology of the plant is not absolutely linked with the single or double chromosome grouping, wide-spread as such association is among algae and other plants.

In the Phaeophyceae this is equally true. In the Ectocarpaceae, for example, gametangial structures of the purilocular type and sporangial structures of the unilocular type are not infrequently simultaneously found on the same plant. The development of sporangia and gametangia is often successional, either seasonal (*Leathesia*) or morphological as in *Myriotrichia*, where sporangia are borne on the creeping parts and gametangia on the erect axes.

However, such cases do not change the general rule that successive cell divisions giving plurilocular reproductive organs are associated with gamogenesis and the plants bearing them are to be considered morphologically as gametophytes, while simultaneous cytokinesis, segregating nuclei from a multinucleate protoplast, is associated with zoöspore production and the plants are morphologically sporophytes. In descriptive morphology and taxonomy they must be so treated or confusion results. The actual physiological behavior of the products of plurilocular and unilocular organs, in relation to sexual or asexual functions and to the production of haploid or diploid individuals, should be kept as a separate problem and not be allowed to confuse the morphological terminology on which the taxonomic arrangement rests.

Parthenogenesis of haploid gametes is reported and when diploid plants produce what morphologically are gametangia, the diploid swimmers therefrom are sexually inert but may reproduce the diploid phase. They are not zoöspores in the sense of the haploid swimmers from unilocular sporangia; they more nearly correspond to the diploid zoöspores produced if meiosis is omitted from sporangial development. On the other hand, sexual functions have

been ascribed to the products of sporangia, but such reports are not so well substantiated except in that old climax group, the Fucaceae. As differences between sporophyte and gametophyte become more marked, the association of form with type of reproductive body and chromosome number becomes more rigid. The shift to the condition seen in the Fucaceae is abrupt, and the group isolated, for we lack stages in the final suppression of a filamentous gametophyte and we lack plants showing a comparable heterospory. It seems that the protoplasmic divisions in the reproductive organs are of the simultaneous rather than the successive type (except for a vestigial wall formation late in antherozooid production), and yet it seems best to consider them as gametangial. We probably can not argue from such a case the plausibility of reports of sexual fusions between products of sporangia (as in Ectocarpaceae) and these reports will have to stand on such merit as confirmatory studies disclose.

TAXONOMIC REVISION

It long ago became clear that the whole systematic structure of the group needed reconsideration, and the writer made some suggestions toward this end in 1920 (32). However, his outline was not sufficiently complete to serve all practical needs and with later research became obsolete. Setchell and Gardner (31) and Kylin (12, 13) in turn offered their preferences, the former essentially from the systematic, the latter from the developmental standpoint. Kylin's more modern version seems to offer a sufficiently broad foundation to serve for a systematic reorganization of the Phaeophyceae. The first necessary change is cancellation of the primary segregation into Phaeosporales and Cyclosporaes as natural orders. Certainly there are additional groups worthy of ordinal rank, and surely the group Cyclosporaes, founded for the Fucaceae, would be artificial if made to include the other oogamous families.

We are offered three classes: Isogeneratae, Heterogeneratae, Cyclosporeae, which last is restricted to the Fucaceae and apparently in an ancient and isolated group.

Isogeneratae.—The Isogeneratae, with sporophyte and gametophyte generations alike in form, and the Heterogeneratae, with the generations different, are not at all clearly characterized. This separation is useful if interpreted as designating tendencies rather

than a completed segregation. Otherwise the terms are misleading. In the Isogeneratae five orders are included. The Ectocarpales includes filamentous or somewhat crustose types with (at least in part) intercalary divisions of the filaments, these almost exclusively transverse. To us *Ectocarpus* is the most familiar genus (7, 8, 17, 29). The Sphacelariales are mostly filamentous, but these filaments grow from prominent apical cells and the segments frequently divide lengthwise in a regular polysiphonous manner (4, 16). Our common genera are *Sphacelaria* and *Cladostephus*. The Cutleriales have trichothallic growth and develop a parenchymatous blade or a disc-like thallus. While *Zanardinia* conforms, *Cutleria* has the sporophyte so much smaller than the gametophyte as to make this order an anomaly in a group called Isogeneratae (12, 27). American representatives are lacking. The Tilopteridales appear morphologically to belong in the Isogeneratae; the plants are filamentous with intercalary growth, but the intercalary gametangia and sporangia show such peculiarities that the degree of sexual evolution is quite uncertain (25). The Dictyotales, which appear to be a climax group, grow like the Sphacelariales from an apical cell or cell row but almost exclusively exhibit a flat blade; they are oogamous. In the sporangia no divisions occur after meiosis and the spores are not motile (5). In the warmer American waters *Dictyota* and other genera are found.

Heterogeneratae.—The Heterogeneratae are divided into subclasses on the basis of their type of growth. On the one hand stands a group with the thallus built up of one or more filaments and their lateral branches (Haplostichineae), and on the other, one with an axis divided and enlarged by longitudinal walls to a parenchymatous structure (Polystichineae). Both these lines show stages in sexual differentiation from isogamy to oogamy. In the simplest order of the Haplostichineae, the Chordariales, the fully developed thallus is usually of the multiaxial type. It bears sporangia in this state and sometimes plurilocular organs which are morphologically gametangia. Since it appears that the structures developed from the zoöspores may be microscopic filamentous plantlets reproducing by gametangia, it is probable that we have a facultative alternation of dissimilar generations in the order (11, 24). However, since the fully developed plants often bear gametangiod structures whose infertility is not universally assured,

and since the diminutive phases often produce the fully developed plants vegetatively, it is quite misleading to assume an obligate alternation. The probability is great that the plants persist without either meiosis or zygois in a diploid state. But for its ponderosity, Sauvageau's noncommittal term of plethysmothalle is more suitable (28). Kylin includes Chordariaceae, Elachisteaceae and Spermatochnaceae in the order, and the genera prominent on our coast include *Chordaria*, *Mesogloia* and *Elachistea* (12, 18, 27).

The Sporochneales are cited as sporangium-bearing in the fully developed plants and as producing plurilocular gametangia on the diminutive phase (22, 23). However, this is known for *Carpomitra* and not for *Sporochneus*, cultures of which have remained sterile. The large plants are morphologically rather specialized, the somewhat club-shaped branchlets bearing tufts of hairs in terminal pits. We find *Sporochneus* in American tropical waters. The climax order of the subclass is the Desmarestiales. In plants of this group there are one or more heavily corticated axial filaments and the branchlets often bear more or less deciduous assimilatory filaments in tufts. Two families are accepted by Kylin: Desmarestiaceae and Arthrocladiaceae (12, 27, 30). Both have microscopic plantlets which in the Desmarestiaceae are definitely said to be oogamous gametophytes but in the Arthrocladiaceae they may have lost their effectiveness. The genera *Desmarestia* and *Arthrocladia* are both found in northern American waters.

The Polystichineae likewise comprise three orders. Throughout, there is a dominant tendency to increase the bulk of the plant by intercalary cell division though filaments do appear in many species in some part of the construction. The Punctariales are reported as having a microscopic phase bearing gametangia; it is to be viewed in much the same light as that of the Chordariaceae, for some plants show gametangioid structures on the massive phase, some show sporangia on the microscopic phase, and the smaller may pass into the larger vegetatively (12, 26). The gametangia are alike and zygois is isogamous; Asperococcaceae, Myriotrichaceae and Striariaceae probably belong in the order, and all families are represented by the typical genera in our northern Atlantic flora.

The Dictyosiphonales are represented by the Dictyosiphonaceae, the only family. The large plants grow from apical cells; segmentation is followed by intercalary divisions. These plants bear

sporangia; the zoöspores develop a filamentous phase which normally appears to be a gametophyte bearing isogametes in small plurilocular gametangia. The alternation ordinarily appears to be an obligate one (12, 26).

The climax of the subclass is the Laminariales (Laminariaceae the only family) where growth is intercalary throughout and extensively parenchymatous, though rudimentary filamentous tissues do persist. Obligate alternation of a microscopic oögamous gametophyte and a very large sporophyte seems general. This is by far the most extensively studied family in the higher algae with respect to life-histories (1, 2, 3, 6, 10, 11, 12, 14, 15, 19, 20, 21). It is a northern family, with *Laminaria*, *Chorda* and other genera on the east coast.

Cyclosporeae.—The final class, Cyclosporeae, also comprises a single order Fucales and family Fucaceae. Growth is initiated by an apical cell group which develops a parenchymatous tissue, often about a filamentous medulla. Fertile areas seem to be progressively restricted toward branch tips or specialized branches, where sporangia are formed in conceptacular pits associated with paraphyses. In the northern flora *Fucus* is common.

The sporangia are dimorphic in arrangement and in size, the larger with one nuclear division after meiosis, the smaller with three. In some cases not all of the megasporangium-derived nuclei persist. The cytokinesis after division segregates 8 cells in the larger sporangia and 32–64 in the smaller. These are discharged, enveloped in the sporangial walls which soften in the water to liberate large motionless cells and small active flagellate swimmers which function as eggs and antherozoids, respectively, the zygote giving rise to the diploid sporophyte. It is obvious that this plant, lacking any independent haploid phase, has an extremely reduced gametophyte. Phanerogams offer an analogous condition.

It seems possible that the evolution of a minute protonemal phase vegetatively continuous which the adult massive gametophyte has been followed by partial and later complete shifting of reproductive fertility from the larger to the smaller stage and finally even the elimination of the large gametophyte. We have no haploid phase in the large form which has sex differentiation evolved to the degree of oögamy, except in the Dictyotales, but this

has apparently occurred independently in all of the lines with reduced gametophytes.

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GLOSSARY

- carposporophyte: a structure among the red algae which arises from fertilization of an egg in a carpogonium by a spermatium and which bears carpospores. The latter produce new plants which in some forms bear sex cells again. In most cases, however, they give rise to plants known as tetrasporophytes which produce asexual tetraspores and these then develop plants which bear sex cells.
- cytokinesis: division of the extra-nuclear portion of the protoplasm.
- gametangia: differentiated cells or cell groups in algal filaments which produce gametes or sex cells.
- gamogenesis: formation of sexual cells.
- heterogamy: the state of male and female sex cells being distinguishable as contrasted with isogamy wherein they are alike and usually motile.
- isogamy: see heterogamy.
- oögamy: the state of differentiation between the sexual cells where the female cells alone completely lack organs of motility.
- Phaeophyceae: the brown algae, one of the great groups of algae, most conspicuous in cold temperate waters.
- plurilocular: many-celled, with reference to sex organs.
- protonema: the thread-like growth issuing from the spores of mosses and upon which the conspicuous plants are developed as lateral or terminal shoots.
- Rhodophyceae: the red algae, one of the great groups of algae, inhabiting primarily temperate and warm waters.
- sporangium: a unicellular structure in the algae within which a spore, or by free cell division several spores, are produced.
- tricothallic: a type of growth characterized by a fringe of hairs along the growing margin or a tuft terminating the branch. Growth proceeds from the meristematic activity of the cells at the bases of these hairs.
- zygosis: fusion of sex cells.

† A complete citation of literature on the relation of structure and life history to the classification of the Phaeophyceae, even if limited to recent papers and the most essential older works, would include 200-300 items. Those cited are merely examples fairly representative of the plants concerned and of the countries in which most of the work has been done. Through the bibliographies which they contain (especially Kylin 1933) most of the important papers can be located.

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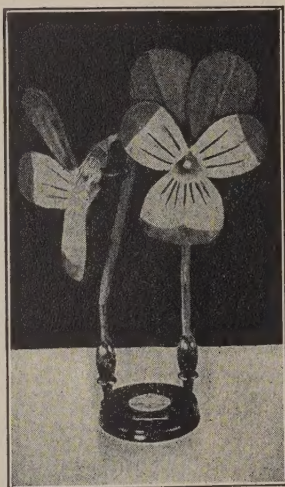
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CHRONICA BOTANICA is published every April as a single volume of about 400 pages, with numerous illustrations, bound in cloth. Annual subscription hfl. 15.-, postage extra. For prospectus, sample pages and further information, apply to the Editorial and Publishing Office, P. O. Box 8, Leiden, Holland.

This year-book is the first and only one of its kind : it contains a vast amount of hitherto unavailable information. It answers hundreds of questions which you have previously had to leave unanswered, though they were of the greatest importance for your work. An annual subscription will well repay you - you cannot afford to be without the latest issue of the "Chronica".

PROGRESS

Our staff is always striving to improve the quality of our products. This is particularly true of the technicians in the microscopic slide division. Not only do they attempt to adapt proposed new technics to commercial and research work, but they have devised several new and useful schedules. Among the latter might be enumerated:

1. Introduction of tertiary butyl alcohol, El Palo Alto brand, for dehydration, with elimination of brittleness and plasmolysis. The schedule is equally adaptable for the paraffin or celloidin technic. The alcohol, incidentally, has a mild ionizing effect, thus permitting more brilliant stain differentiation. It is the least expensive of all dehydrating fluids.

2. Introduction of a new fluid for dehydration of materials intended for mounting entire in balsam. The technic is so simple that beginning students in microtechnique have readily made perfect mounts of *Spirogyra*. The fluid will soon be on the market.

3. Adaptation of Harris's hematoxylin for whole mounts of many plant objects, such as fern prothallia, the red algae, certain fungi.

4. Perfection of a method of ionizing tissues previous to staining. Difficulties caused by killing fluids, dehydrating fluids, overabundant cell inclusions, etc., are completely eliminated.

5. Refinement of Hance's rubber-paraffin concoction, with the addition of petroleum ceresin, to provide the nearly perfect embedding medium. Pure Ceylon latex is used as the basis. This medium, called Parlax, is available at an unusually low price.

A Preserved Materials catalog and list of macerated woods and other plant organs are now in course of preparation.

There have, of course, been failures and disappointments. The faults of dioxan, for instance, were found to outweigh its virtues and its use has been abandoned.

Copies of our Microscope Slide Catalog have been mailed to all colleges and universities in the United States and Canada. If one is not available, we shall be happy to send one on request.

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